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PATTERNS OF GEOGRAPHIC VARIATION IN THE ARABIAN WARBLER *SYLVIA LEUCOMELAENA* (AVES: SYLVIIDAE)

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Abstract.—The distribution and relationships of *Sylvia leucomelaena,* a species generally found in *Acacia* parkland, are reviewed. Analysis of seven morphological and two plumage characters results in the recognition of three subspecies: *S. l. leucomelaena* (Hemprich & Ehrenberg) from western Saudi Arabia, the Yemens, and the Dhofar region of Oman; *S. l. somaliensis* (Sclater & Mackworth-Praed) from Somalia and Eritrea; and *S. l. blanfordi* Seebohm from southeastern Egypt and eastern Sudan. Birds inhabiting the Arava of southern Israel are closest to nominate *leucomelaena* but differ in several characters. A phytogeographical analysis is presented of the origin, dispersal, and modern distribution of this habitat, and how it relates to the present patterns of geographic variation in *S. leucomelaena.*

Of the 15 species in the Palearctic genus *Sylvia* Scopoli, the Arabian or Blanford's Warbler, *S. leucomelaena,* is the only one breeding south of the Sahara (Watson et al. 1986). Its nesting range includes portions of southern Israel, the Arabian Peninsula, and the African Red Sea mountains and coastal plain, generally in relatively dense *Acacia* parkland. This habitat consists of widely dispersed clusters of trees, often in remote and relatively undisturbed country. Except for a recent study in southern Israel virtually nothing is known about the Arabian Warbler's natural history and ecology. To date, no published study has examined patterns of geographic variation in this species.

In the course of a 1985 biological survey of Gebel Elba in the Red Sea Mountains of southern Egypt, just north of the Sudanese border, a population of *S. leucomelaena* was discovered and a small series collected. Before a subspecific designation could be placed on this material it was necessary to review patterns of geographic variation in this species. The purpose of this paper is to describe these patterns and to present a phytogeographical analysis that may account for them. Information is also given on distribution, sexual dimorphism, several aspects of natural history, and taxonomic conclusions.

Materials and Methods

Seven measurements were taken from museum specimens (all in mm): Wing—measured from the bend of flattened wing at carpal joint to longest primary tip. Tail—measured between the insertion of central tail rectrices to distal tip. Exposed culmen—measured from base of feathering on the forehead to maxilla tip. Bill from nostril—measured from anterior edge of nostril to maxilla tip. Bill width—measured across upper mandible at anterior edge of nostril. Gonys—measured from junction of rami to maxilla tip. Tarsus—measured from the junction of tibiotarsal-tarsometatarsal joint to distal edge of distal most undivided scute overlying the toes (little variation was found in the scale pattern of the feet). A rule was used to the nearest 1.0 mm for the wing and tail measurements and a dial calipers to the nearest 0.1 mm for the other measurements.

Since virtually no information is available in the literature on the weight or food habits of *S. leucomelaena* this information, based on field and museum studies, is summarized herein. Weights of the Egyptian specimens were taken to the nearest 0.1 gm. All other weight data are from museum specimens and the unpublished field notes of Mr. G. Nikolaus or Mr. M. C. Jennings. All references to altitude are presumed to be m above sea-level.

Four specimens were selected as standards for comparison of crown-color. These are (darkest to lightest): BMNH 1925.11.20.26, male, Sogsode, Somalia; BMNH 1919.12.17.702, male, Erkowit, Sudan; BMNH 1915.12.24.720, female, Erkowit, Sudan; and BMNH 1919.12.17.686, female, Sinkat, Sudan. The contrast between the crown and back did not enter into the selection of these standards. Four standards were used to quantify the amount of white on the outer pair of rectrices (Fig. 1). Individual specimens were compared to these standards and scored accordingly.

Statistical tests used MIDAS programs, written by the University of Michigan Statistical Research Laboratory. Differences among means and variances were tested by Student's *t*-test or analysis of variance (ANOVA), as appropriate. Scheffé tests were also used in pairwise combinations to test differences in means between geographical regions. Probabilities of 0.05 or less are considered statistically significant and sufficient to reject the null hypothesis that the means are equal.

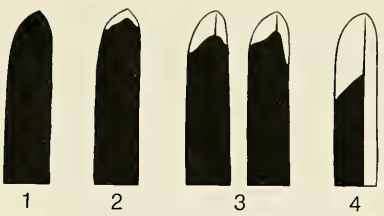

Fig. 1. Four standards used to quantify the amount of white on the outer pair of rectrices.

Review of *Sylvia leucomelaena* Taxonomy

The original description of *S. leucomelaena* by Hemprich & Ehrenberg (1833) was based on material taken in Arabia. They placed the bird in genus *Curruca.* In a review of Hemprich and Ehrenberg specimens in the Berlin Museum, Dresser & Blanford (1874) described the type of *S. leucomelaena,* gave measurements and noted this species resemblance in details to *Sylvia rueppelli.* In 1878 Seebohm described *Sylvia blanfordi* based on a single specimen taken at Rairo, Habab, Abyssinia (=Eritrea). Although he cited the paper of Dresser and Blanford, Seebohm believed that the Rairo specimen represented a new species, with some similarity to *S. curruca, S. melanocephala* and *S. rubescens* (=*S. mystacea*).

In a review of birds collected in the Yemens, Hartert (1917) named a subspecies, *Parisoma blanfordi distincta.* His placement of this form in *Parisoma* was unexplained but may have been due to the notion of his time that the Palearctic and the Afrotropical (=Ethiopian) biogeographic realms were completely distinct. It would thus have been difficult to explain a *Sylvia* breeding in sub-Saharan Africa.

Sclater & Mackworth-Praed (1918) described the new form *somaliensis* from material collected at Mundara, Somalia, and retained this species in *Parisoma.* Their diagnosis noted that *somaliensis* was distinguishable from *blanfordi* and *distincta* by its smaller size and differences in back coloration and tail pattern. Meinertzhagen (1949) reviewed this situation and considered *Curruca leucomelaena* and *Sylvia blanfordi* conspecific. Further, he presented evidence that the species should be shifted from *Parisoma* to *Sylvia.*

Afik & Pinshow (1984) questioned the allocation of this species to *Sylvia,* primarily on several aspects of natural history, and suggested a reexamination of its generic position. As pointed out by Dowsett-Lemaire

& Dowsett (1985), however, little comparative natural history information is currently available on most Afrotropical Sylviidae. Furthermore, the genus *Sylvia* shows a remarkable degree of plasticity in aspects of life history, and such characters probably provide little information on the naturalness of the group.

General Distribution of *Sylvia leucomelaena* by Country

ISRAEL—In April 1972 this species was found nesting in the Arava (Rift Valley), 10 km south of the southern end of the Dead Sea (Zahavi and Dupai 1974) (Fig. 2). In more recent years it has been observed in relatively dense *Acacia tortilis* and *A. raddiana* stands from the southern end of the Dead Sea south to within 40 km of Eilat (Afik & Pinshow 1984; H. Shirihai, pers. comm.).

SAUDI ARABIA—The Arabian Warbler is a breeding resident of southwestern and western Saudi Arabia, often in areas with thick vegetation such as along the Tihama (Stagg 1985). Hutchinson (1975) reported several observations from central Saudi Arabia near Riyadh; these records were rejected by Jennings (1981). Meinertzhagen (1954) designated the type locality of *Curruca leucomelaena* Hemprich & Ehrenberg as Midian (perhaps Maidn Salah, 26°45′N, 37°55′E; Jennings 1981), a northern area of the country for which there are no modern records (M. C. Jennings, pers. comm.).

THE YEMENS—During a trip to North Yemen from 7–29 Apr 1979 Cornwallis & Porter (1982) recorded this species on nine occasions in the Western Ramparts and Highland Plateau between 500 and 1700 m, invariably in *Acacia* groves. This species is a fairly common but local resident of the Tihama foothills, particularly in *Acacia/Commiphora* bushland (Brooks et al. 1987).

SULTANATE OF OMAN—The Arabian Warbler is known from Dhofar, in the southwestern corner of the Sultanate, where it tends to occur "on hillsides and in mountain wadis" (Gallagher & Woodcock 1980: 252). In this region it has been recorded in every month of the year and is considered a breeding resident (Gallagher 1986). The Oman distribution of the Arabian Warbler is exceptional. In some regions it inhabits areas of mixed woodland, without extensive tracts of *Acacia* spp. (M. D. Gallagher, pers. comm.).

SOMALIA TO ERITREA—Archer and Godman (1961) noted that this species occurs in Somalia along the coastal plain and plateau between sea-level and up to about 1800 m, and as far south as Galoli and Burao. More recently it has been presumed to be a "fairly common" resident in the northern portion of Somalia above 8°30′N in acacias along the coastal plain and up to the plateau beyond the coastal mountains (Ash & Miskell 1983:59). This species has been noted throughout portions of Djibouti, particularly in *Acacia* scrubland (G. Welch, pers. comm.). Smith (1957) noted that the Arabian Warbler was found in the Red Sea coastal hills of Eritrea, at least between Massawa and Dankalia, generally in deep wadis below 320 m and with acacia cover.

SUDAN—Cave & Macdonald (1955:255) listed this species as a "rather uncommon resident of the old Red Sea Province."

EGYPT—In early 1985 this species was discovered in the immediate vicinity of Gebel Elba (22°11′N, 36°21′E), Sudan Government Administration Area (Goodman & Meininger in press a). Although no nests were found, numerous singing males were observed in the dense *Acacia* groves and clear territorial interactions noted. Five adult specimens were collected, all of which had enlarged gonads. This species is presumed to be a local breeding resident in the Gebel Elba area. There are no specimen records from elsewhere in the country (Goodman and Meininger in press b); although it is plausible it occurs in extreme eastern Sinai just across the border from known Israeli populations.

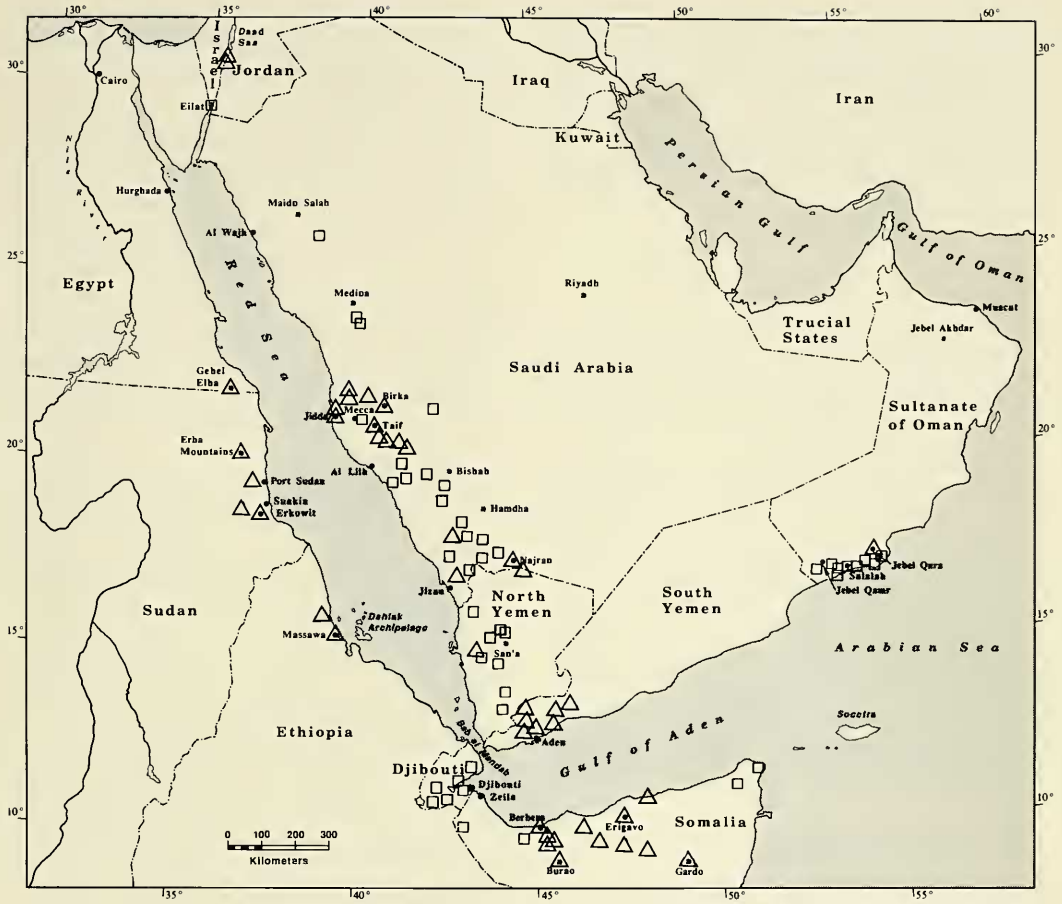

Fig. 2. Distributional map of *Sylvia leucomelaena* across its complete range. Open triangles represent specimens examined and open squares sight records from the literature or unpublished information.

Notes on the Recently Discovered Egyptian Population

The Egyptian population of *S. leucomelaena* appears to be limited to the slopes and valleys of Gebel Elba in the extreme southeastern corner of the country. This mountain, which rises to 1428 m, is unique for Egypt in that a significant portion of the plants and animals are of Afrotropical rather than Palearctic origin. The Gebel Elba area has relatively heavy vegetation and contains dense *Acacia* parkland (Kassas & Zahran 1971). *Acacia tortilis* is common along the coastal plain, foothills and lower slopes of Gebel Elba, and *A. raddiana* on the north slopes and in valleys bisecting the southern slope (Kassas & Zahran 1971).

The Arabian Warbler was observed at various sites around the mountain but was more common on the northern side, where the *Acacia* parkland is most extensive. Generally they were observed singly or in pairs. The first territorial aggression was noted on 13 Apr 1985, although songs were heard soon after our arrival in February. Interspecific encounters were recorded on several occasions. On 13 April one adult *S. leucomelaena* was noted flying in a mixed flock of three *Cercomela melanura* and six *Sylvia melanocephala*. Later that same day one adult *S. leucomelaena* was observed chasing

a male *S. melanocephala.* On 14 April four adult *S. leucomelaena* were noted foraging in a mixed flock with *S. curruca* and *Cercomela melanura.* In the Gebel Elba area *Cercomela* is a local breeding resident and *Sylvia curruca* and *melanocephala* migrants and winter visitors.

Results

Sexual dimorphism in measurements.—No single geographically constant pattern of sexual dimorphism was found in this species (Table 1). Morphological differences were not detected between the sexes in the Arava or in the combined Somalian and Eritrean samples. Only a single female was available from the Gebel Elba, Egypt, population and no statistical comparison was made; however, for all seven measurements the value of the female fell within the range of males from this locality. In both the Saudi Arabian and Yemen samples, males have statistically longer wings and tails than females. Sudanese males have longer wings than females.

Sexual dimorphism in plumage coloration within geographic regions.—In the Saudi Arabian, Somalian/Eritrean and Sudanese samples, adult males have darker crowns than adult females (Table 2); the contrast was most notable for Sudanese birds. These sexual differences are statistically significant. No sexual variation was found in this character for the Yemen, Arava or Egyptian populations, although in the latter two cases the sample size was limited. Within the various geographical regions sexual difference was found in tail pattern only in the Saudi Arabian sample (Table 3), in which males tend to have more white on the outer rectrices than females (P = 0.018).

Geographic variation in plumage coloration.—No statistically significant difference between regions was found in the head coloration of adults, whether partitioned by sex or lumped together. For the tail pattern the situation is more complex. Since no sexual variation was found in this character for any population inhabiting the western side of the Red Sea, the sexes were combined in this analysis. In this region there is clinal variation in the tail pattern. Adult birds from Egypt have less white on the outer rectrices (n = 5, mean = 2.0) than Sudanese (n = 21, mean = 2.9, P = 0.0001), and Sudanese birds have less white than Somalian/Eritrean (n = 27, mean = 3.9, P = 0.0001). The pattern on the eastern side of the Red Sea is similar with an increasing amount of white on the tail from north to south, but the range of variation is not as great, perhaps in part due to small samples from some areas. Scores were only available from the Arava population for adult females. These birds have less white on the outer rectrices (n = 2, mean = 2.0) than Saudi Arabian females (n = 10, mean = 2.2) and Yemeni females (n = 7, mean = 2.4). None of these comparisons showed statistical significance. Males from Saudi Arabia had slightly more white (n = 15, mean = 2.7) than those from Yemen (n = 8, mean = 2.6). The single male from Oman has a tail score of 2. No difference was found between the Arava and Egyptian populations.

Geographic variation in morphology.—Since the wing and tail measurements of adult males and females are dimorphic in two populations they were partitioned within each sample (Table 4). No differences were found between birds from Saudi Arabia and Yemen, and these populations are combined in subsequent analyses. The wing lengths of both male and female populations living on the west side of the Red Sea are similar to one another; the only exception is that males from the Sudan have slightly longer wings than males from the Somalia/Eritrea sample (F = 5.98, P = 0.017).

There is considerable variation in tail length among the five geographic areas. Within either sex class no significant variation was found between the Egyptian and Sudanese samples; however, when these

samples were compared to birds from Somalia/Eritrea differences were found in both cases (Table 4). Males from Arava have longer tails than those from the Arabian Peninsula ($F = 4.05$, $P = 0.048$), while females are similar to one another. Within each sex class there is a cline in tail length on both sides of the Red Sea, decreasing in size from north to south.

Sylvia leucomelaena from Arava have substantially wider bills than the other four samples (Table 5). There appears to be clinal variation in bill width on the western side of the Red Sea, decreasing in size from north to south.

Analysis of the exposed culmen measurement showed a unique pattern of variation (Table 5). Significant differences were found in the Sudanese birds relative to those from the Arabian Peninsula ($F = 21.60$, $P = 0.0000$), Somalia/Eritrea ($F = 33.54$, $P = 0.0000$), and Egypt ($F = 15.15$, $P = 0.0002$). This variation shows no clear clinal pattern. The bill length from nostril also revealed an unusual pattern of variation (Table 5); the statistically significant differences were between the Arabian Peninsula and Somalia/Eritrea samples ($F = 7.97$, $P = 0.005$), the Arabian Peninsula and Sudan samples ($F = 4.28$, $P = 0.04$), and Somalia/Eritrea and Sudan samples ($F = 19.28$, $P = 0.0000$).

The gonys length of Sudanese birds was the smallest of any of the samples and statistically different from all others, except the Egyptian birds (Table 5). A comparison of F-statistics for tarsus length was not included in Table 5. The only statistically significant difference was between the Somalia/Eritrea and Egyptian samples ($F = 5.50$, $P = 0.03$), which most likely reflects two extremes of a cline.

Weight.—Weights from three adults handled by Mr. Michael C. Jennings at Hejaz, Saudi Arabia, in mid-May 1976 are 14.8, 15.3, and 16.3 g. For 29 unsexed autumn birds weighed by Mr. Gerhardt Nikolaus during ringing operations near Erkowit, Sudan, the mean weight was 13.9 g and range 12.5–16 g, excluding one bird which weighed 9 g. Four weights are available for wild birds from the Arava population, two adult males at 15 and 13.5 g, and two adult females at 16 (with "full grown egg") and 15 g (UTM). Weights of Egyptian birds include: five males—mean 12.3 g and range 11.2–13.2 g, and one female—12.5 g (UMMZ).

Food.—Meinertzhagen (1954) considered the Arabian Warbler an insectivore. Afik & Pinshow (1984) reported that it searched acacia bark for larvae, hawked flying insects, and dug for small insects on the ground under acacia. They further noted that this species frequently eats ripe fruits of three perennial shrubs: *Nitraria retusa, Lycium shawii* and *Ochradenus baccutus.*

Of the five specimens taken at Gebel Elba, Egypt (UMMZ), three had empty stomachs and two contained unidentified fruits. Two birds collected at Sinkat, Sudan (BMNH), had seeds in their stomachs and no insects, while a third contained berries. One bird from Somalia (LSUM) had Coleoptera remains in the gizzard.

Discussion

The East African Rift Valley, the Red Sea, Gulf of Aqaba, and the Arava are portions of a single tectonic system, often referred to as the Afro-Arabian Rift Valley. The shearing of the Red Sea apparently commenced in the early Miocene (Ross & Schlee 1973), as the Arabian plate drifted away from the African plate. This rifting activity continued with varying intensity through the upper-most Miocene or lowest Pliocene, at which time the southern Red Sea opened into the Indian Ocean (Hötzl 1984). Presently, the Red Sea is a little under 2000 km long. The southern strait at Djibouti, Bab el Mandab, is about 30 km wide. In the north the average width varies from 150 to 180 km and between 15° and 18°N the sea widens to 350 km. The Gulf of Aqaba is about 170 kms long and varies between 15 and 30 km in width.

Table 1.—Sexual differences in seven morphological characters in adult *Sylvia leucomelaena*.[1]

	Wadi Arava		Saudi Arabia		Yemen		Somalia and Eritrea		Sudan		Egypt	
Measurement	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Wing												
n	2	3	15	9	10	7	22	10	18	8	4	1
Range	73–74	67–72	68–77	67–72	68–72	66–71	63–72	65–68	65–70	65–67	65–68	65
Mean	73.5	70.0	71.5	69.2*	70.2	68.1*	66.0	66.3	67.6	65.9**	66.3	
SD	0.71	2.65	2.69	1.64	1.39	2.04	1.88	1.06	1.42	0.83	1.50	
Tail												
n	2	3	13	7	10	7	21	10	17	8	4	1
Range	69–71	62–68	64–71	60—68	63–68	60–65	56–67	56–63	59–65	60–63	61–65	63
Mean	70.0	64.7	67.4	65.0**	65.5	62.4**	59.0	59.5	62.4	61.4	62.5	
SD	1.41	3.06	2.53	2.58	1.58	2.37	2.65	2.37	2.06	0.92	1.91	
Exposed culmen												
n	2	3	15	9	10	7	20	9	18	8	4	1
Range	11.4–12.0	10.7–11.2	10.6–12.7	9.6–12.4	10.5–12.2	11.8–12.0	10.9–12.8	10.9–12.7	10.1–11.7	10.0–11.8	11.5–12.4	11.6
Mean	11.70	11.03	11.52	11.48	11.37	11.87	11.71	11.71	10.89	10.89	12.03	
SD	0.42	0.29	0.55	0.76	0.51	0.09	0.55	0.56	0.58	0.54	0.41	
Bill width												
n	2	3	15	9	10	7	20	9	18	8	4	1
Range	3.2–4.3	3.8–4.5	2.8–3.4	2.8–3.2	2.5–3.5	3.1–3.6	2.8–3.5	2.9–3.2	2.7–4.4	2.7–3.1	3.1–3.4	3.2
Mean	3.75	4.06	3.09	3.04	2.96	3.28	3.09	3.09	3.28	2.94	3.23	
SD	0.78	0.38	0.18	0.10	0.30	0.19	0.18	0.13	0.53	0.12	0.15	
Gonys												
n	2	3	15	9	10	7	22	10	18	8	4	1
Range	7.1–8.2	6.8–8.8	7.2–8.9	6.6–8.3	7.0–8.2	7.2–8.7	6.9–8.7	7.3–8.7	6.4–8.0	6.7–7.9	7.0–8.0	7.0
Mean	7.65	7.87	7.79	7.61	7.59	7.72	7.71	7.92	7.38	7.30	7.53	
SD	0.78	1.01	0.42	0.47	0.44	0.59	0.44	0.47	0.43	0.35	0.41	
Bill from nostril												
n	1	2	15	9	10	7	20	9	14	8	4	1
Range	8.5	8.3–9.4	8.0–9.8	7.2–9.2	7.8–9.3	7.8–9.1	8.0–9.4	8.3–9.3	7.5–8.8	7.8–8.8	8.2–9.0	8.4
Mean		8.85	8.54	8.69	8.43	8.29	8.75	8.90	8.16	8.36	8.60	
SD		0.78	0.45	0.66	0.48	0.42	0.42	0.36	0.38	0.35	0.34	

Table 1.—Continued.

Measurement	Wadi Arava		Saudi Arabia		Yemen		Somalia and Eritrea		Sudan		Egypt	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Tarsus												
n	1	2	15	9	10	7	22	9	14	8	4	1
Range	22.2	22.0–22.6	21.2–23.0	20.8–24.5	20.8–24.0	20.5–22.8	20.1–23.6	20.8–22.7	21.0–23.1	21.5–22.8	21.7–24.4	22.0
Mean		22.30	22.07	22.36	22.14	21.96	21.87	21.59	22.05	22.19	22.88	
SD		0.42	0.58	1.18	0.98	0.89	0.91	0.60	0.68	0.38	1.26	

[1] Sexual differences between the means were tested with Student's *t*-test, one asterisk $P < 0.05$, two asterisks $P < 0.01$.

Table 2.—Percentages of adult *Sylvia leucomelaena* within a geographic region scored for different head color standards.[1]

Region	Standard (dark to light) 1	2	3	4	Mean
Arava					
Male (n = 1)	0.0	100.0	0.0	0.0	2.0
Female (n = 1)	0.0	100.0	0.0	0.0	2.0
Saudi Arabia*					
Male (n = 15)	6.7	80.0	13.3	0.0	2.1
Female (n = 10)	0.0	70.0	30.0	0.0	2.3
Yemen					
Male (n = 8)	0.0	90.0	10.0	0.0	2.1
Female (n = 7)	0.0	57.1	28.6	14.3	2.6
Somalia and Eritrea*					
Male (n = 20)	15.0	80.0	5.0	0.0	1.9
Female (n = 8)	0.0	62.5	37.5	0.0	2.4
Sudan***					
Male (n = 14)	7.1	92.9	0.0	0.0	1.9
Female (n = 8)	0.0	25.0	62.5	12.5	2.9
Egypt					
Male (n = 4)	25.0	75.0	0.0	0.0	1.8
Female (n = 1)	0.0	0.0	100.0	0.0	3.0

[1] Within a geographical region sexual differences between the means of the two sexes were tested with Student's *t*-test, one asterisk $P < 0.05$, three asterisks $P < 0.001$.

As mentioned earlier, *Sylvia leucomelaena* is generally confined to relatively dense *Acacia* groves, and its distribution seems to partially coincide with that of *A. tortilis* and *raddiana*. Both of these trees often occur sympatrically and their local distribution is adjusted to the local micro-climate. *A. tortilis* is adapted to higher temperatures and dryer conditions than *raddiana*; while *raddiana* is more tolerant of a wider range of temperature and moisture (Halevy and Orshan 1972). The exception to this apparent habitat requirement is in Oman, where the bird occurs in mixed open woodland areas of the Dhofar region.

Zohary (1962) hypothesized that before the Miocene *A. tortilis* and *raddiana* migrated from Africa along the eastern coast of the Red Sea across to and north along

Table 3.—Percentages of adult *Sylvia leucomelaena* within a geographic region scored for different tail pattern standards.[1]

Region	Standard 1	2	3	4	Mean
Arava					
Female (n = 2)	0.0	100.0	0.0	0.0	2.0
Saudi Arabia*					
Male (n = 15)	0.0	26.7	73.3	0.0	2.7
Female (n = 10)	0.0	80.0	20.0	0.0	2.2
Yemen					
Male (n = 8)	0.0	37.5	62.5	0.0	2.6
Female (n = 7)	0.0	57.1	42.9	0.0	2.4
Somalia and Eritrea					
Male (n = 19)	0.0	0.0	5.9	94.1	3.9
Female (n = 8)	0.0	0.0	12.5	87.5	3.9
Sudan					
Male (n = 14)	0.0	0.0	100.0	0.0	3.0
Female (n = 7)	0.0	14.3	85.7	0.0	2.9
Egypt					
Male (n = 4)	0.0	100.0	0.0	0.0	2.0
Female (n = 1)	0.0	100.0	0.0	0.0	2.0

[1] Within a geographical region sexual differences between the means of the two sexes were tested with Student's *t*-test, one asterisk $P < 0.05$.

western Arabia, to the Gulf of Aqaba, into the Arava and other portions of the Levant. Given our present knowledge of plate tectonics of this area, these two land masses would have been at least partially connected at that time. Shmida & Or (1986) presented a strong case that the invasion of these plants into the Arava, although along the same route suggested by Zohary, has been since the end of the Pleistocene, long after the shearing took place. Their argument is primarily based on the low degree of local endemism in these Afrotropical elements, their wide distributional disjunctions, and adaptations to arid conditions and long-distance dispersal. In either case, the modern range of *Acacia* spp. in the mountains and along the coastal plains bordering the Red Sea is evidence to support this dispersal route, whether it took place before or after rifting, and most importantly how this distribution is relevant to that of *Sylvia leucomelaena.*

Several species of *Acacia* are common along the western Red Sea coastal plain from the East African Rift Valley (Beals 1970), north through Eritrea (Hemming 1961), to the Red Sea Mountains of Sudan (Kassas 1956, 1957). Just north of the Egyptian/Sudanese political border, near Gebel Elba, nine *Acacia* spp. are known to occur; these are dominated by *tortilis* and *raddiana* (Kassas & Zahran 1971, Täckholm & Boulos 1972, Täckholm 1974). North of Gebel Elba, in the Egyptian Eastern Desert, there

Table 4.—Comparison of *F*-statistics by geographic region for two sexually dimorphic characters in adult *Sylvia leucomelaena,* wing length (upper right corner) and tail length (lower left corner).[1]

Region	1	2	3	4	5
1		3.09	26.12***	16.16***	18.14***
		1.57	10.64**	14.78***	7.46**
2	4.05*		68.02***	29.82***	19.67***
	0.42		10.75**	17.55***	5.27*
3	43.29***	118.18***		5.98*	0.03
	13.76***	22.41***		0.62	0.79
4	19.37***	31.20***	23.00***		1.56
	4.44*	5.24*	4.69*		0.27
5	13.88***	10.25**	9.15**	0.13	
	0.39	0.09	2.84	0.44	

[1] For each matrix the numbers on top within a geographic region comparison are males and below females. 1 = Arava, 2 = Arabian Peninsula (combined Saudi Arabia, Yemen, and Oman), 3 = Somalia and Eritrea; 4 = Sudan, 5 = Egypt. One asterisk $P < 0.05$, two asterisks $P < 0.01$, three asterisks $P < 0.001$.

Table 5.—Matrices of *F*-statistics by geographic region for non-sexually dimorphic characters in adult *Sylvia leucomelaena*.[1]

Geographic area	Bill width/exposed culmen					Bill from nostril/gonys				
	1	2	3	4	5	1	2	3	4	5
1		0.75	2.91	2.12	3.47		0.16	0.85	3.99*	1.60
2	37.04***		2.96	21.60***	2.64	0.69		1.91	10.51**	1.67
3	33.77***	0.07		33.54***	0.52	0.09	7.97**		18.10***	3.79
4	27.40***	2.01	1.13		15.15**	2.78	4.28*	19.28***		0.12
5	13.64**	1.31	0.98	0.17		0.28	0.05	1.38	1.65	

[1] Character to left of slash is on bottom half of matrix, character to right of slash is on top half of matrix. 1 = Arava, 2 = Arabian Peninsula (combined Saudi Arabia, Yemen, and Oman), 3 = Somalia and Eritrea, 4 = Sudan, 5 = Egypt. One asterisk $P < 0.05$, two asterisks $P < 0.01$, three asterisks $P < 0.001$.

are only small patches of *Acacia raddiana* and most of the other species fall out (Kassas & Imam 1959; Kassas & Zahran 1962, 1965; Boulos & Hobbs 1986). This is compared to the eastern side of the Red Sea, where relatively dense *Acacia* parkland occurs along the Arabian Peninsula coastal plain and above the Tihama in the Asir and Hejaz Mountains (M. C. Jennings, pers. comm.); forming a more or less continuous band from East Africa across to and along the eastern edge of the Arabian Peninsula (Vesey-Fitzgerald 1955, 1957). Based on the present distribution of *Acacia* along the western side of the Red Sea (including the Gulf of Suez), it appears that contiguous tracts have not existed in this region in the recent geological past; precluding the possibility that these trees migrated through this pathway into the Levant. Clearly, this is based on the assumption that the modern distribution of *Acacia* in this area parallels that since the end of the Pleistocene, and that changes in climatic patterns and human land-use have not resulted in the extinction of areas of *Acacia* parkland. The main point of this phytogeographical analysis is that evidence exists that *Acacia* spp. spread from East Africa into the Levant via the Arabian Peninsula, and that a habitat corridor existed along this pathway for dispersal from the northern Afro-Arabian Rift Valley into East Africa.

Seventeen species of *Sylvia* are known to occur in Africa (Vaurie 1959, Etchécopar & Hüe 1967, Moreau 1972, Watson et al. 1986). Of these, eleven have breeding populations on the continent. (This figure includes *S. sarda,* but see Thomsen & Jacobsen 1979.) For the most part the breeding ranges of the other ten species are restricted to the Mediterranean Sea coastal zone, in areas receiving about 100 mm of precipitation per year and basically with a Palearctic flora; a few species also occur south into coastal Mauritania. The exceptions are *S. nana deserti* and *S. deserticola* which penetrate into portions of the western Sahara; the latter species is endemic, as is the subspecies *S. melanocephala norrisae* known from the Faiyum of Egypt. Excluding *leucomelaena,* none of these *Sylvia* occur in areas with Afrotropical biota and the habitat of their African breeding range is basically an extension of what they use in Eurasia.

Several workers have speculated that *hortensis* and *leucomelaena* form a superspecies, are part of the same subgenus, or each others closest relatives (Hall & Moreau 1970, Wolters 1980, Watson et al. 1986). Four subspecies of *hortensis* are currently recognized (Vaurie 1959, Watson et al. 1986), three of which are important for this review: nominate *hortensis* breeds in portions of central Europe and North Africa from Morocco to Tripolitania (western Libya), and winters in portions of the Sahara and north-

ern sub-Saharan Africa; *crassirostris* breeds in eastern and southeastern Europe, the Middle East and Cyrenaica (eastern Libya), and winters in east Africa; and *balchanica* breeds in Transcaspia and Iran and winters in Arabia. Given the variety of ecotypes used by *hortensis,* ranging from temperate forest and high mountain country during the breeding season to desert scrub during the winter, and its close relationship with *leucomelaena,* it seems plausible for the latter form to have adapted to one of these habitats, namely *Acacia* parkland. Throughout much of the Arabian and east African wintering grounds *hortensis* occurs in scrubland, often sympatrically with *leucomelaena*; for example, in the *Acacia* plains of coastal Eritrea (Moreau 1972).

Remembering that the genus *Sylvia* is of Palearctic origin, and that *leucomelaena* is the only *Sylvia* breeding in sub-Saharan Africa, it is presumed that *leucomelaena* speciated in the northern portion of the Afro-Arabian Rift Valley, then spread along the *Acacia* corridor of the western Arabian Peninsula, and then crossed over the Red Sea (presumably at the narrows in the south) into east Africa. Once in Africa it spread north through the Red Sea Mountains and coastal plain until it reached the northern limit of dense *Acacia* groves. The modern sympatric occurrence of *leucomelaena* and *hortensis* during the winter months in portions of Arabia and eastern Africa is presumably secondary contact after the events of speciation and dispersal. The possibility that a population of the proto-modern *hortensis/leucomelaena* group wintering in east Africa became resident, speciated and spread northwards on both coasts of the Red Sea cannot be eliminated. However, this seems unlikely since no parallel exists for any other *Sylvia* species, the majority of which winter at least in part in Africa.

Taxonomic Conclusions

Sylvia l. leucomelaena.—Meinertzhagen (1949) noted that the head and mantle colors of nominate *leucomelaena* were paler than African birds. This conclusion is generally supported by the present study. Since several populations are sexually dimorphic in head coloration it is important to analyze this character only within a sex class. Some of Meinertzhagen's other color comparisons were confounded by not taking this factor into account. Birds from the Arabian Peninsula, including Yemen and Oman, tend to have less white on the outer pair of rectrices than African birds, particularly those from Somalia/Eritrea.

Specimens from the Arava differ from Arabian Peninsular birds in several ways: less white on the outer pair of rectrices (although the Arava sample consisted of only two birds); males have longer tails; and both sexes have substantially wider bills. These differences seem to warrant subspecific separation of the Arava population. However, the naming of a new form is suspended until further data are available.[1]

Sylvia l. distincta.—No consistent difference was found between birds from the Yemens and the balance of the Arabian Peninsula. *S. l. distincta* is a synonym of *S. l. leucomelaena.*

Sylvia l. somaliensis.—Populations from Somalia and Eritrea are easily recognizable from all others by the large amount of white on the outer pair of rectrices. No consistent difference was found in head coloration between these populations and other African populations or those from the Arabian Peninsula (cf. Meinertzhagen 1949).

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[1] Shirihai, H. 1988. A new subspecies of Arabian Warbler *Sylvia leucomelaena* from Israel.—Bulletin of the British Ornithologists' Club 108:64–68, has recently proposed the name *Sylvia leucomelaena negevensis* for the Arava population. A copy of the current paper was sent to Mr. Shirihai on 26 June 1987 for his comments. In subsequent correspondence he made no mention that a manuscript describing this subspecies was in preparation and never provided the reciprocal courtesy of reviewing it. His paper was received by the Bulletin of the British Ornithologists' Club on 10 August 1987.

Sylvia l. blanfordi.—Morphologically the Gebel Elba, Egypt, and Sudanese populations seem similar to one another, or differences are part of a north-south cline. The only exception is that Gebel Elba birds have distinctly longer exposed culmens than Sudanese birds; however, the degree of difference may be partially an artifact of the small number of Egyptian birds available for comparison. Egyptian and Sudanese birds tend to have a shorter gonys. Both of these populations have significantly less white on the outer pair of rectrices than those Somalian/Eritrean. No important difference was found in head coloration among any of the African populations.

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Appendix 1

Material of *Sylvia leucomelaena* Examined

Museum codes: AMNH, American Museum of Natural History, New York; BMNH, British Museum (Natural History), Tring; HH, Private collection of Haim Hovel, Haifa; LSUM, Louisiana State University Museum, Baton Rouge; SGM, Sudan Government Museum, Khartoum; UMMZ, The University of Michigan Museum of Zoology, Ann Arbor; UTM, Zoological Museum, University of Tel Aviv, Tel Aviv; YPM, Yale Peabody Museum, New Haven; ZFMK, Zoologisches Forschungsinstitut und Museum Koenig, Bonn.

Israel.—Km 20 on Arava Road, UTM 8088, 8089; Yotvata, HH 82110, 82112, ZFMK 8416; Hatzeva, UTM 8153.

Saudi Arabia.—Al Jurf, BMNH 1936.6.29.20–23 (4); Ashaira (Asheira, Ushayeah), BMNH 1935.1.5.81–82 (2); Bir Askar, Taif Plateau, BMNH 1935.1.5.78–79 (2); Bir Braman (Burayman), 15 km NE Jidda, BMNH 1940.4.1.24; Birka, BMNH 1950.58.2; Farha, BMNH 1935.1.5.80; Hadda, Wadi Fatima, BMNH 1936.6.29.18–19 (2); Hamdha, upper Wadi Tathlith, BMNH 1937.4.17.275; Hejaz (al Hijaz), BMNH 1946.69.76–77 (2); Jidda (Jedda), 10 miles E., BMNH 1934.9.20.140–142 (3), 1937.12.26.15; Khadra, Najran, BMNH 1937.4.17.273, 1937.4.17.277; Madriga (Madrakah), nr. Jidda, BMNH 1965.M.13775; Wadi Hafra, 80 km NE Jidda, BMNH 1940.4.1.25; Wadi Harjab, Wadi Bisha, BMNH 1937.4.17.276, 1948.58.29; Wadi Hijla, BMNH 1946.69.78; Wadi Jaura, Tihama, Jizan, BMNH 1937.4.17.22; Wadi Krarrar, near Taif, BMNH 1949.5.33.

The Yemens.—Al Kubar (el Kebir), Amiri Dist., South Yemen, BMNH 1903.8.12.25, AMNH 608810; Dhala (Dthala), Amiri Dist., South Yemen, BMNH 1903.8.12.26, 1965.M.13777; Gerba, Amiri Dist., South Yemen, BMNH 03.8.12.21–24 (4), AMNH 608806 (type of *distincta*), 608807–809 (3); Habil, South Yemen, BMNH 1965.M.13776; Jajeilha, Yemen, AMNH 608811; Jebel Manif, north of Lahej, South Yemen, BMNH 1900.8.5.193; Lodar (Lawdar), South Yemen, BMNH 1965.M.13778; Ma'ir, Abian, South Yemen, BMNH 1900.8.5.194; Tullah, Hadhramaut, South Yamen, BMNH 1932.4.20.5; Wadi Awa, Hadhramaut, South Yemen, BMNH 1933.6.26.6; Wadi Khabb (Khubb), southeast Najran, Yemen, BMNH 1937.4.17.274; Wadi Thibi, South Yemen, BMNH 1937.6.5.81.

Oman.—Khadrafi, Jebel Qamr, Dhofar, BMNH 1977.1.10.

Somalia.—Berbera Plain, BMNH 98.7.27.80; Bihendula (Bikendula), AMNH 608789–90 (2); Burao (Buraa), BMNH 1923.8.7.3038; Dubar, AMNH 608803–805 (3), BMNH 1905.11.27.164–165 (2); Erigavo, BMNH 1965.M.13773, LSUM uncataloged (2); Galoli, BMNH 1923.8.7.3036; Gardo, BMNH 1945.10.11; Gidial (Gidil) Valley, Golis, AMNH 608800, BMNH 1923.8.7.3035; Las Khorai (Khoreh), AMNH 608791–792 (2); Mush Haled (Mush Aled, Musha Aled, Mash Caleed), Warsangli, 200 miles E. Berbera, AMNH 608793–794 (2), YPM 32258; Mundara (Mandara), BMNH 98.6.13.76 (type of *somaliensis*); Sogsode (Sogsoda, Suksodi, Sugsade), BMNH 1923.8.7.3037, 1925.11.20.26, AMNH 608795–797 (3); Waghar (Wagr, Wogr), AMNH 608801–802 (2), BMNH 1905.11.27.168–169 (2).

Eritrea.—near Massawa, BMNH 1952.25.19; Rairo, Habab, BMNH 69.10.16.85 (type of *blanfordi.*).

Sudan.—Erba Mountains, BMNH 97.10.15.3; Erkowit, BMNH 1915.12.24.719–720 (2), 1916.9.20.671, 1919.12.17.700–703 (3), SGM 686, 2034, 2773, 3286; Port Sudan, BMNH 1965.M.13774; Sinkat, BMNH 1919.12.17.683–699 (17).

Egypt.—Wadi Aideib, Gebel Elba, UMMZ 224089–091 (3); Wadi Akwamtra, Gebel Elba, UMMZ 224092; Wadi Kansisrob, Gebel Elba, UMMZ 224088.